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EXPANDING THE PALPI OF MALE SPIDERS'

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INTRODUCTION

Genitalia and secondary sexual structures are important in the determination of spiders to the species level. This is especially true in the male, where the palpus has become modified as an intromittent organ. In many genera, the females are virtually inseparable into species, and small differences in shape, size, relative position, and complexity of the parts of the highly modified and specialized male palpus are used to distinguish between closely related species of a genus.

In families where the male palpus is highly specialized, the palpal organ has become so folded and convoluted that some parts are hidden in the normal retracted palpus. While these parts are not always of taxonomic importance, they nevertheless need to be examined in detail, especially in characterizing new species.

Many publications concerned with spider taxonomy include figures of male palpi that have been treated in order to unfold or to expand the organ. In other publications, figures are of untreated and unexpanded palpi and, as a result, confusion and uncertainty arise in comparing species and in making identifications, because frequently there are striking differences between expanded and unexpanded palpi of the same species. In an expanded palpus, sclerites, which are hidden in an unexpanded palpus, are revealed and the serial relationship of the sclerites becomes more apparent.

My purpose is not to decide what parts of the palpus are of value in taxonomy, but merely to determine what additional parts can be seen when the palpi of representative species are expanded.

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METHODS

In *The Spider Book*, Comstock (1940, p. 111) described a process for expanding the complex palpal organs of male spiders. This method was probably the one used by Comstock in preparing specimens for a 1910 paper on spider palpi, because the text of the 1910 publication is the same as the section on palpi in *The Spider Book*. The method he described involves immersing the palpus in boiling 10 per cent "caustic" for 10-15 minutes. After treatment, the palpus is rinsed in water and preserved in glycerine.

Engelhardt (1910) challenged this method on the grounds that the boiling solution was somewhat destructive. He was working on the more delicate female genitalia at that time. In 1925, Petrunkevitch, in a similar study, concluded that Engelhardt's objections were not substantiated by results, and further stated that palpi prepared by boiling corresponded closely to those he

observed in actual use by the male spider.

Gering (1953) prepared a large series of palpi using boiling potassium hydroxide solution, but for studies of the natural mode of expansion placed preserved palpi in concentrated potassium hydroxide solution for a few minutes before a rapid transfer to distilled water, where the palpi were inflated by osmotic pressure.

Levi (1961) used hot sodium hydroxide solution, followed by distilled water. Osmotic pressure expanded the organ. In 1965, he suggested the use of boiling 85 per cent lactic acid solution, on the grounds that it is far less destructive than sodium hydroxide solution. He also mentioned that satisfactory results can be obtained by using fine needles and forceps to expand the parts of the palpal tarsus.

The method used in this study was similar to that used by Gering (1953) and Levi (1961). Palpi removed from specimens preserved in 70 per cent ethanol solution were placed in 10 per cent KOH solution for 6-8 hours at room temperature and were completely expanded in distilled water. The expanded palpi were then returned to alcohol.

Twenty-nine species, distributed among 22 genera and 10 families of higher spiders, were selected as test samples on the basis of the number of specimens available, completeness of taxonomic definition, and number of available references. Also, each of these species has palpi similar in degree of complexity to the palpi of a number of other species and genera in their respective families.

Before expanding the palpus of one of the species, a number was assigned and placed in the vial containing the specimens. In most cases, the right palpus of an individual was removed and treated, leaving the left as a control, but in some small species. the whole male was treated to avoid damage to the palpus in removal. After expansion, the palpus (or the whole specimen) was placed in alcohol in a separate vial and labelled with the same number as was previously assigned. The vial containing the palpus was then bound to the original vial of specimens with a rubber band. These specimens in alcohol were used in making the freehand drawings and in writing the descriptions.

TERMINOLOGY

The course taken by the evolution of secondary sexual structures in spiders is open to speculation. Comstock (1940), Barrows (1925), Savory (1928), Gertsch (1949), Alexander and Ewer (1957), and Levi (1961) have expressed ideas on the subject. Until we can be reasonably certain of the phylogeny of the sclerites of the male palpus, names applied to these scierites do not necessarily indicate homologies.

Comstock (1940) effectively reviewed previous research on spider palpi and devised a system of terminology widely accepted by most authors. Comstock's terminology will be followed in this

study.

The following description refers to the expanded palpus of

Araneus sericatus (Clerck) (Figs. 20, 21).

The segments of the palpus proximal to the tarsus are only rarely modified. In most spiders, the coxa of the palpus bears an endite that functions as a mouth part, crushing and straining food material. The trochanter can bear a small projection of unknown function. The femur of the palpus of a male spider is sometimes furnished with sclerotic picks, which rub against stridulating areas on the sides of the chelicerae, producing squeaking or barking noises. Gering (1953) demonstrated in the genus *Agelenopsis* that apophyses on the tibia and patella can serve as locking devices in copulation.

It is the palpal tarsus, especially the tarsal claw, that has been strongly modified (Barrows, 1925). The body of the tarsus has become modified in males of the more specialized families to form a cup-shaped cymbium (cy), the cavity of which is the alveolus. The cymbium is basal in position and the palpal organ itself folds into the alveolus when at rest (Figs. 18, 19). The most proximal portion of the organ is called the basal division. Actually attached to the wall of the alveolus is a hollow, bladder-like structure termed the basal hematodocha (bh). The cavity of the basal hematodocha is continuous with that of the cymbium, allowing the hematodocha to be inflated by increasing blood pressure. At the distal end of the basal hematodocha is a smooth or annulated ring of sclerotic material, the subtegulum (st).

The middle division consists of the tegulum (t), an inappropriately named ring of heavily sclerotized tissue connected to the subtegulum by the middle hematodocha (mh). Articulated with the tegulum is a usually small sclerite, the median apophysis (ma). In some male spiders, this appears as a knob or process on the

tegulum.

The apical division is the most complex of the three divisions. The embolus (e) is the functional part of the organ, bearing at its tip the opening of the ejaculatory duct. The conductor (c) is a usually membranous outgrowth from the base of the embolus, serving to protect the embolus. The radix (r) and stipes (s) are small, and are often absent in less complex palpi. Both radix and stipes arise near the base of the embolus, although they may appear more distal. The palpal organs in some families do have parts of the organ actually distal to the embolus. These parts include a distal hematodocha (dh) and the lateral subterminal apophysis (lsa). The terminal apophysis (ta) is located at the very tip of the organ.

OBSERVATIONS

Order ARANEAE Family THERIDIIDAE

The theridiids, or comb-footed spiders, have recently been the subject of an extensive revision by Levi from 1952 to 1964. In

1961, Levi published his ideas on the evolution of the palpal organ in this large and complex family, and concluded that the original type of palpus was probably simple, that most members of the Theridiidae have a complex palpal organ, and that secondary simplification can be seen in some otherwise highly specialized theridiids.

For my purposes, I selected four species that represent various degrees of complexity within the family.

Steatoda borealis (Hentz)

Figs. 1, 2, 3

Levi (1957a) gives excellent figures of the palpus of *Steatoda* borealis in his revision of the genus *Steatoda*. Both expanded and unexpanded palpi are shown, and some individual sclerites are figured.

In a mesal view of the unexpanded right palpus (Fig. 1), the embolus (e) can be seen, but the basal portion is hidden. The conductor (c), and the radix (r), both of which support the embolus in this species, are fairly obvious, but the shape of the radix is obscured by other sclerites lying over its ectal part. In a mesal view of an expanded right palpus (Fig. 2), the rotate base of the embolus (e) is exposed, and its true relationship to the conductor and radix (r) is revealed. In an ectal view of the same palpus (Fig. 3), expansion has caused a general ectad rotation of all the sclerites, bringing the median apophysis (ma) from behind overlying sclerites.

Enoplognatha tecta (Keyserling) Figs. 4, 5

When Levi (1957b) revised the genus *Enoplognatha*, he gave two figures of an unexpanded palpus and one of an expanded

palpus of this species.

In an ectal view of an unexpanded left palpus (Fig. 4), the median apophysis and subtegulum are completely covered by overlying sclerites, although the shape of the embolus (e) and its relationship to the conductor (c) and radix (r) are obvious. In an ectal view of an expanded palpus (Fig. 5), the median apophysis (ma) has been rotated ectad and ventrad and the subtegulum (st) is visible. In both Figures 4 and 5, the hooklike projection of the anterior portion of the cymbium (cy) is seen. This is the paracymbial hook, which in some families is developed as a separate sclerite.

Theridion differens Emerton

Figs. 6, 7

Levi (1957b) reviewed the genus *Theridion*, a very large and geographically widespread assemblage of, in many cases, remarkably similar species. Levi did not figure an expanded palpus of *Theridion differens*, although he figured expanded palpi of several other species of the genus.

When an unexpanded right palpus in ventral view (Fig. 6) is compared with an expanded right palpus (Fig. 7) seen from the same aspect, it is clear that little more is visible after expansion.

Theridion frondeum Hentz Figs. 8, 9

This species is figured by Levi in his revision of *Theridion* (1957b). As in *Theridion differens*, an expanded palpus (Fig. 9) shows very little that is not readily visible in the unexpanded palpus (Fig. 8).

Family LINYPHIIDAE

Recent literature on this family has been restricted to a few occasional papers describing new species and giving new distributional records (Chamberlin and Ivie, 1943; Gertsch and Davis, 1946; Gertsch, 1951; and others). Blauvelt (1936) studied the palpus of *Linyphia*.

Because the palpi of members of this family are somewhat uniformly complex, two of the more common species were selected

for this study.

Drapetisca alteranda Chamberlin Figs. 10, 11

In a mesal view of an unexpanded right palpus (Fig. 10) of Drapetisca alteranda, the paracymbium (pc) is seen as a free sclerite, loosely articulated with the cymbium (cy). The lateral subterminal apophysis (lsa) is highly developed and forms a shield covering the entire palpal organ. In a mesal view of an expanded right palpus (Fig. 11), the general ectad rotation caused by expansion is readily noticed. Parts, including the subtegulum (st) and tegulum (t), which were completely hidden before treatment, are now easily seen. The bulky base of the embolus (e) is now visible, and the shape of the lateral subterminal apophysis (lsa) is more satisfactorily observed.

Linyphia marginata C. L. Koch Figs. 12, 13

In this species, studied by Blauvelt (1936), the lateral subterminal apophysis (lsa), as seen in an ectal view of the unexpanded right palpus (Fig. 12), is not so highly developed as it is in the complex shield of Drapetisca. The tegulum (t) and subtegulum (st) are at least partially visible, but the conductor (c) and embolus (e) are obscured. In an ectal view of an expanded right palpus (Fig. 13), an ectad rotation brings into clearer view the position of the median apophysis (ma), which seems much more distal in the unexpanded palpus. and the exact shape and size of the unusually heavy embolus (e). The conductor (c) is readily observed, with its supporting sclerotic bar along one side. The lateral subterminal apophysis (lsa) is reflexed, appearing as if it were proximal, rather than distal, to the embolus.

Family MICRYPHANTIDAE

This family has not been studied as a unit since the publication of a long series of papers by Crosby, Crosby and Bishop, and Bishop and Crosby from 1905 to 1938 (listed by Kaston, 1948). Because of the seemingly simplified structure of the male palpus, there is some controversy about the proper taxonomic position of the Micryphantidae. The family is such a large one and shows so many degrees of palpal complexity that it would be impossible to treat the Micryphantidae satisfactorily in a paper of this nature. A recent study by Merrett (1963) of the palpal anatomy of this family treats the Micryphantidae as the subfamily Erigoninae of the Linyphiidae, but Merrett's work was confined to British species.

The species I studied were selected on the basis of their intermediate type of palpal organ.

Soulgas corticarius (Emerton) Figs. 14, 15

This species was treated by Crosby and Bishop (1936), who gave a figure of an unexpanded palp, along with the characteristic

cephalic modification found in this group.

An ectal view of an unexpanded right palpus (Fig. 14) shows the obviously simple structure, including a free paracymbium (pc), subtegulum (st), tegulum (t), and embolus (e). The shape of the tibia (ti) is unusual, having a modification that in at least some degree occurs in all male micryphantids. In mesal view, an

expanded right palpus (Fig. 15 shows two features that cannot be seen in an unexpanded palpus. The great development of the basal hematodocha (bh) is obvious. A small sclerite (ma) possibly represents a rudimentary median apophysis.

Ceratinopsidis formosa (Banks) Figs. 16, 17

Bishop and Crosby (1930) published a figure of the unexpanded palpus of *Ceratinopsidis formosa*. The unexpanded palpus (Fig. 16) has features similar to those of *Soulgas corticarius*. In an expanded palpus (Fig. 17) observed in dorsoectal view, the greatly developed basal hematodocha (*bh*) is seen, but no sclerite corresponding to a median apophysis is apparent.

Family ARANEIDAE

Archer (1951, p. 3) defined this family as follows:

"Paracymbium vertical or divergent from the axis of the cymbium, but its basal face not resting on the apical face of the tibia, instead usually being separated from it by a distinct gap. Attachment of the genital bulb to the cymbium ranging from universal-median and then by all degrees of migration to frankly basal (as in the Theridiidae). Tegulum greatly overbalancing the subtegulum, the latter ranging from ring-like to a vestigial knob. Position of the cymbium and genital bulb normal."

If the Araneidae are considered in the strict sense, excluding the Tetragnathidae and the Theridiosomatidae, then all members of the family have complex palpi, but some do show various degrees of reduction in certain sclerites. I selected eight fairly representative species.

Araneus sericatus Clerck Figs. 18, 19, 20, 21

The complicated palpus of this species was described in the section on TERMINOLOGY. In a ventral view of the unexpanded right palpus (Fig. 18), little can be seen except the subtegulum (st), tegulum (t), terminal apophysis (ta), and median apophysis (ma). In mesal view (Fig. 19), some additional structures are visible, but their relationships to definitely identifiable structures are obscure. A number of interesting structures are revealed in an ectal view of an expanded right palpus (Fig. 20). The anterior portion of the subtegulum is completely unsclerotized, so that the basal and middle hematodochae (bh, mh) are

fused anteriorly. The tegulum (t) is a heavy rounded structure articulating closely with the large median apophysis (ma). The parts of the embolic subdivision are visible distal to the tegulum. The spatulate stipes (s) and small conductor (c) articulate with the base of the embolus (e), but the radix (r) has been displaced proximad. In a mesal view of the same palpus (Fig. 21), the hook-like lateral subterminal apophysis (lsa) is fused with the large plate of the terminal apophysis (ta), and both are separated from the embolic subdivision by the distal hematodocha (dh).

Araneus nordmanni (Thorell)

The palpus of *Araneus nordmanni* is very similar in general plan to that of *Araneus sericatus*, differing only in the shape and position of some of the sclerites. Expansion in this species has the same effect as expansion has on the palpus of *Araneus sericatus*.

Argiope trifasciata (Forskal) Figs. 22, 23

The main difference between the palpus of this species and those of species of the genus *Araneus* lies in the reduction of some of the sclerites of the embolic subdivision.

In a mesal view of an unexpanded right palpus (Fig. 22), the subtegulum is not seen, but in its place a portion of the basal hematodocha (bh) appears as the most basal part. The tegulum (t), embolus (e), and well-developed conductor (c) are all readily visible. The median apophysis (ma) is large and has a serrated ventral edge. In a dorsomesal view of an expanded right palpus (Fig. 23), the subtegulum (st) has been moved into view. The ectad rotation of the median apophysis (ma) has revealed a small hook on the dorsal surface. The embolus (e) and conductor (c) are fused for about two-thirds of their length. Other sclerites of the embolic subdivision seem to be absent, although the swollen base of the embolus possibly represents a reduced radix.

Araniella displicata (Hentz) Figs. 24, 25

Chamberlin and Ivie (1942) removed this species from *Araneus* and made it the type species of their new genus *Araniella*. Unfortunately, they did not present figures of the type species.

I studied the palpus in detail. In an ectal view of an unexpanded right palpus (Fig. 24), the subtegulum (st) appears cupped, as if it has taken on the function of the conductor in this species. The very large tegulum (t) is easily visible. The basal part of the embolus (e) seems to be fused to the tegulum. The basal part of the median apophysis (ma) is hidden by the cymbium (cy). In an ectal view of an expanded right palpus (Fig. 25), the reduction of the subtegulum (st) characteristic of this family, as described by Archer (1951), is clearly seen. The basal part of the median apophysis (ma) is visible and there is a small "hematodocha" around the base of the embolus (e) and median apophysis. This area of lightly sclerotized tissue may represent a vestigial distal hematodocha, but due to the absence of any sclerites morphologically distal to the embolic subdivision, this "hematodocha" is best considered an articulating membrane between the tegulum (t) and the median apophysis.

Singa pratensis Emerton Figs. 26, 27

The members of the genus *Singa* are structurally close to the theridiids (Kaston, 1948), but the structure of the palpus is closer to *Araneus* than are some species formerly considered to be in *Araneus*. According to Kaston (1948), who figures the palpus and epigynum, the species of *Singa* resemble one another so closely in form and appearance that they can be separated only

by examining the external genitalia.

By comparing a mesal view of an unexpanded right palpus (Fig. 26) with the palp of *Araneus sericatus* (Fig. 19), one sees that the relative sizes of the structures correspond closely. The subtegulum (st) is reduced. The tegulum (t), median apophysis (ma), and terminal apophysis (ta) are all visible. The expanded right palpus in ectal view (Fig. 27) bears close resemblance to the expanded palpus of *Araneus sericatus* (Fig. 20). The sclerites of the embolic subdivision are all visible in essentially the same positions as in *Araneus sericatus*, but the radix of *Araneus sericatus* is in a slightly different position (Fig. 21).

Neoscona arabesca (Walckenaer)

The genus *Neoscona* is closely allied to *Araneus*. The males bear complex palpal organs built around the general *Araneus* plan. Expansion delineates the relationships of the various sclerites in much the same way as in *Araneus sericatus*, *Araneus nordmanni*, and *Singa pratensis*.

Mangora gibberosa (Hentz) Figs. 28, 29

Mangora gibberosa has a complex palpus that, due to the displacement of the sclerites, seems even more complex than it really is. In an ectal view of an unexpanded right palpus (Fig. 28), the subtegulum (st) is visible and is large for a member of the family Araneidae. The tegulum (t) and terminal apophysis (ta) are separated by a large radix (r), the sheet-like, membranous conductor (c), and the enlarged base of the embolus (e). In a ventroectal view of an expanded right palpus (Fig. 29), the hematodochae seem to appear very much reduced, and most of the sclerites occupy positions different from those of the previously described araneids. In addition, the conductor is much enlarged.

Cyclosa conica (Pallas)

Kaston (1948) gave a figure of the palpus of the male of Cyclosa conica. In the degree of palpal complexity and reduction of hematodochae, this species lies somewhere between Argiope trifasciata and Mangora gibberosa. As in Mangora, the sclerites are much displaced, making them difficult to identify. Expansion causes an ectad rotation and further displacement, but, after treatment, individual sclerites can be seen as entities and at least tentatively identified. The median apophysis is bifurcate, as in many araneids, and the distal lobe is sigmoid. As in Mangora, the conductor is large and membranous and interferes with identification of the sclerites in the unexpanded palpus.

Family AGELENIDAE

The genitalia of some agelenids have been studied intensively with regard to their form and function (Gering, 1953). The palpus is moderately complicated, with a reduced subtegulum and a well-developed conductor that serves, at least in *Agelenopsis*, as a locking device during copulation (Gering, 1953).

Wadotes calcaratus (Keyserling) Figs. 30, 31, 32

Muma (1947) revised the genus *Wadotes* and figured only individual sclerites rather than complete palpal organs. He considered the terminal apophysis to be of unusual value in taxonomic decisions.

In a ventral view of an unexpanded right palpus (Fig. 30), the subtegulum (st), tegulum (t), and embolus (e) are easily seen, as is the terminal apophysis (ta). In an ectal view of an expanded right palpus (Fig. 31), the distal portion of the embolus (e) is extensive and threadlike. Muma (1947) refers to the embolus as lying along a distinct conductor, but it seems to me that the only structure one can suggest as a conductor is solidly fused to the terminal apophysis. In a mesal view of an expanded right palpus (Fig. 32), the feature most noticeable is the distinctly annulated subtegulum (st).

Coras lamellosus (Keyserling)

Muma (1946) revised the North American members of the genus *Coras* and figured the palpi of a number of species, including *Coras lamellosus*. The palpus is very much like that of *Wadotes calcaratus* in the general arrangement of sclerites. After expansion, a general ectad rotation brings the long, thin embolus into full view. The conductor can be seen as separate from the terminal apophysis, and there is a twisted median apophysis that before expansion was concealed by the conductor and terminal apophysis.

Agelenopsis utahana (Chamberlin and Ivie) Figs. 33, 34

This is one of the species used by Gering (1953) in a monumental study of the structure and function of the external genitalia of the genus *Agelenopsis*, and he gives several very useful

figures of the expanded palpus.

In an ectal view of the unexpanded right palpus (Fig. 33), the embolus (e) is seen to be long, heavy, and spirally coiled. The tegulum (t) is somewhat indented to accommodate the embolus. In a mesal view of an expanded right palpus (Fig. 34), the fused basal and middle hematodochae (bh-mh) are visible. The subtegulum (st) has been pushed into view, and the conductor (c) has rotated mesad. Gering (1953) refers to the basal part of the embolus as the radix, and this may be morphologically correct.

Tegenaria domestica (Clerck) Figs. 35, 36

Tegenaria domestica is a common house spider often referred to as Tegenaria derhami (Scopoli), and its habits have been studied extensively. The legs and palpal segments of this species are elongate.

In a ventral view of the unexpanded right palpus (Fig. 35), the cymbium (cy) bears a long distal finger. The tegulum (t), median apophysis (ma), and embolus (e) are fused into one sclerite capping the hematodochae. In an ectoventral view of an expanded right palpus (Fig. 36), the fused basal (bh) and middle hematodochae (mh) are inflated. The "cap" has been rotated ectad, and the hook-like conductor (c) has been extended on a short articulating membrane. No subtegulum was evident in this palpus, but an area on the basal hematodocha that is more heavily sclerotized than the rest of the hematodocha may correspond to the subtegulum.

Cicurina robusta Simon Figs. 37, 38

Exline (1936) and Chamberlin and Ivie (1940) examined representatives of the genus *Cicurina*, and both gave excellent figures, concentrating on the tibia, which in males of this genus is uniquely developed. Frequently they neglected to provide figures of the palpal organ itself.

In an ectal view of an unexpanded left palpus (Fig. 37), the hooked conductor (c), the radix (r), and the embolus (e) are all visible, at least in part. The unusual tibial apophysis (ti) extends up the ectal side of the cymbium (cy). In an ectal view of an expanded right palpus (Fig. 38), the flattened subtegulum (st) has become visible, and the cupped tegulum (t) accommodates the radix (r) and the base of the embolus (e). The long and spirally wound embolus tapers to a hairlike tip. The hooked conductor (c) is extended.

Family LYCOSIDAE

This is a large and homogeneous family of which *Lycosa* is the principal genus. The palpi of most lycosids are similar to one another in general plan.

Lycosa ammophila Wallace

Wallace (1942) studied the *lenta* group of the genus *Lycosa* and described a number of new species, including *Lycosa ammophila*, from southeastern United States. Wallace gave figures of the palpus in ventral view, but emphasized the median apophysis, which he also figured separately in outline. In the unexpanded palpus, most of the features are readily visible. Expansion does, however, clarify relationship among the sclerites.

Family CLUBIONIDAE

The palpi of this family are simple, except for those of certain genera belonging to the subfamily Liocraninae and none of these are considered here. The palpal organs of most liocranines are similar to those of the Agelenidae.

Clubiona bryantae Gertsch Figs. 39, 40

Gertsch (1941) proposed *Clubiona bryantae* as a new name for *Clubiona agrestis* Emerton, but he gave no figures. The new name was accepted by Edwards (1958), who gave several figures

of the male palpus.

In an ectal view of an unexpanded right palpus (Fig. 39), the subtegulum (st), tegulum (t), and embolus (e) are subequal. The expanded right palpus (Fig. 40) shows the ectad rotation of the embolus (e), exposing its fingerlike tip.

Aysha gracilis (Hentz) Figs. 41, 42

Aysha and a number of related genera (Anyphaena, Anyphaenella, Gayenna, and others) are often placed in a separate family, the Anyphaenidae, on which no recent work has been done.

In a ventral view of an unexpanded right palpus (Fig. 41), the tegulum (t) is large and extends below the alveolus or cavity of the cymbium (cy). The embolus (e) has a large, rotate, flattened base, and then tapers to a fine point, cupped by a projection of the cymbium. In a mesal view of an expanded right palpus (Fig. 42), all the parts appear to have been pushed cctad, and the subtegulum (st) is now visible. The track of the internal sperm duct through the tegulum is prominent.

Family SALTICIDAE

The Salticidae is considered by some authorities to contain the most advanced of spiders (Kaston, 1948), but the palpi are highly simplified.

Metacyrba undata (De Geer) Figs. 43, 44

In a ventral view of an unexpanded right palpus of *Metacyrba* undata (Fig. 43), little is visible except the tegulum (t), which is enlarged and greatly extended proximally into a hollow on the

ventral surface of the palpal tibia (ti), and the fused embolusconductor (e, c). In the ectodorsal view of an expanded palp (Fig. 44), the basal hematodocha (bh) is large and displaces all the sclerites ectad. The subtegulum (st) is visible as a small, sclerotic ring.

Tutelina elegans (Hentz) Figs. 45, 46

Kaston (1952) gave figures showing the general appearance of this species, but he did not illustrate the genitalia. In a ventral view of an unexpanded right palpus (Fig. 45), the general appearance is essentially the same as in *Metacyrba undata*, but no recognizable conductor is present on or near the embolus (e). Expansion of the palpus (Fig. 46) brings about an ectad rotation and, in an ectodorsal view, the subtegulum (st) is exposed.

Salticus scenicus (Clerck)

This species is distributed throughout the United States and Europe and has been widely studied. The palpus is very simple and follows the general plan of the two previously described species of the family Salticidae. In the expanded palpus, the basal hematodocha is greatly expanded, and the subtegulum is brought into view.

Family ULOBORIDAE

This family was recently revised by Muma and Gertsch (1964), and a number of new species were described. Figures were given of unexpanded palpi and individual segments, but an error was made in the figure titles.

The palpi of these spiders are remarkable for the extreme development of certain sclerites. The habits of the Uloboridae are unique, but among some species the modes of web-building converge with those of the Araneidae. This behavioral convergence is not reflected in the morphology of the palpal organs of the males.

Hyptiotes cavatus Hentz Figs. 47, 48, 49

Muma and Gertsch (1964) illustrate the entire palpus of *Hyptiotes cavatus* and also give a figure of what they call the "tip of the embolus." Close examination of actual specimens and of the textual description given by Muma and Gertsch leaves little doubt

that this figure actually represents the tip of the median apophysis.

In an ectal view of an unexpanded right palpus (Fig. 47), the most striking feature is the large, elongated median apophysis (ma) with its membranous tip. The tegulum (t) and subtegulum (st) are almost completely covered by the enlarged membranous conductor (c). The embolus (e) originates mesally and coils around the other sclerites of the palpal organ. In a mesal view of the same palpus (Fig. 48), the origin of the embolus (e), as well as its attenuated distal part entering the conductor (c), is easily seen. The conductor is accompanied by the long, hooked radix (r). An ectoventral view of an expanded right palpus (Fig. 49) shows that expansion has resulted in little change, but the whole of the distal part of the embolus (e) can now be seen and its relationship to the median apophysis (ma) is clear.

Family DICTYNIDAE

Chamberlin and Gertsch (1958) revised this family, of which *Dictyna* is the largest genus. While the palpal organs of all North American species of *Dictyna* are similar, Chamberlin and Gertsch separated species on the basis of the structure of the tip of the embolus.

Dictyna sublata (Hentz) Figs. 50, 51

In a mesal view of an unexpanded right palpus (Fig. 50) of Dictyna sublata, the embolus (e) appears heavy and coiled and distally enters the large shieldlike conductor (c). The path of the sperm tube can be traced through the tegulum (t) and the base of the embolus. A ventral view of an expanded right palpus (Fig. 51) shows that an almost complete ectad rotation of the base of the embolus has occurred. The subtegulum (st), as well as the basal and middle hematodochae (bh, mh), is visible.

DISCUSSION

For purposes of discussion, the males of species used in this study can be separated into three groups: those with very complex palpi, those with moderately complex palpi, and those with simple palpi.

Drapetisca alteranda, Linyphia marginata, Araneus sericatus, Araneus nordmanni, Neoscona arabesca, Cyclosa conica, Singa pratensis, Mangora gibberosa, and Hyptiotes cavatus fall in the

group having very complex palpi. In this group almost all possible sclerites are present in a more or less highly developed form. These species are especially characterized by the number of sclerites distal to the embolus. Males of species of *Drapetisca* and *Linyphia* have palpi in which the lateral subterminal apophysis is developed into a large shield covering the whole organ. In species of *Araneus* and *Singa*, the male palpus has many structures concealed by other sclerites and by the manner in which the palpus is folded. In males of *Mangora*, *Cyclosa*, and *Hyptiotes* displacement of the sclerites has caused confusion when unexpanded palpi are used in the description of species. Expanding the palpus can

be of great value in this group.

In the group with moderately complex male palpi are: Enoplognatha tecta, Theridion differens, Theridion frondeum, Steatoda borealis, Argiope trifasciata, Araniella displicata, Wadotes calcaratus, Agelenopsis utahana, Coras lamellosus, Cicurina robusta, Lycosa ammophila, and Dictyna sublata. This group is characterized by the approximately equal development of most sclerites. The apical division is poorly represented, and some of the sclerites of the embolic subdivision are reduced. Usually the basal hematodocha is well developed. When the palpus is moderately complex, one has to use his own judgment whether or not expansion will be worthwhile. The process of expansion has the value of making relationships clear and exposing portions of sclerites that may be hidden, because in most species in this group the full complement of sclerites (except the subtegulum) is usually visible before expansion.

The third group, species with simple male palpi, includes: Soulgas corticarius, Ceratinopsidis formosa, Tegenaria domestica, Clubiona bryantae, Aysha gracilis, Metacyrba undata, Salticus scenicus, and Tutelina elegans. These spiders have palpi characterized by the loss, fusion, or reduction of sclerites. Expansion

seems to be of little utility in this group.

The process of expansion seems to have its greatest value in studying species with complex palpi. The complex palpus may indicate specialization and occurs in three very highly specialized families (Theridiidae, Linyphiidae, Araneidae). However, spiders of a fourth very specialized family, the Salticidae, have a simple type of palpus.

If the hematodochae of a complex palpus are reduced, expansion does not show structures that were not visible in the unexpanded palpus. In such cases, a delicate dissection of the palpus

may be indicated. The need for expansion may also be partly obviated by the presence of other taxonomically useful sexual modifications, such as the ornate third leg of some salticid males or the tibial apophyses and cephalic modifications of the micryphantids.

SUMMARY

- 1. Several methods have been suggested for expanding the palpi of male spiders for taxonomic purposes. The method used in this study involved immersing the palpus for 6-8 hours in a 10 per cent KOH solution, followed by a quick transfer to distilled water. Expanded palpi were stored in 70 per cent ethanol solution.
- The expanded palpus of each of 29 species of spiders was compared with the unexpanded palpus of the same species to determine if any parts not observable in the unexpanded palpus could be seen in the expanded palpus.

The process of expansion was found to be most useful in species with complex palpi and least useful in species with simple palpi.

4. Under certain conditions, such as the reduction of hematodochae, many features of complex palpi were still obscure.

5. The experimenter must use his own judgment in deciding when the process of expansion is worthwhile, but certainly more detailed examination of palpi after expansion can be of benefit in the present confused state of spider taxonomy.

LITERATURE CITED

ALEXANDER, A. J., and D. W. EWER.

On the origin of mating behavior in spiders. Amer. Natur. 91: 311-317.

ARCHER, A. F.

Studies in the orbweaving spiders (Argiopidae). 1. Amer. Mus. Novit. No. 1487: 1-52.

BARROWS, W. M.

Modification and development of the arachnid palpal claw, with especial reference to spiders. Ann. Entomol. Soc. Amer. 18: 483-516.

BISHOP, S. C., and C. R. CROSBY.

Studies in American spiders: genera Ceratinopsis, Ceratinopsidis, and Tutaibo. J. New York Entomol. Soc. 38: 15-34.

BLAUVELT, H. H.

The comparative morphology of the secondary sexual organs 1936. of Linyphia. Festschr. Embrik Strand 2: 81-171.

CHAMBERLIN, R. V., and W. J. GERTSCH

1958. The spider family Dictynidae in America north of Mexico. Bull. Amer. Mus. Natur. Hist. 116: 1-152.

CHAMBERLIN, R. V., and W. IVIE

1940. Agelenid spiders of the genus *Cicurina*. Bull. Univ. Utah, Biol. Ser. 5(9): 1-108.

1942. A hundred new species of American spiders. Bull. Univ. Utah, Biol. Ser. 7(1): 1-117.

1943. New genera and species of North American linyphiid spiders. Bull. Univ. Utah, Biol. Ser. 7(6): 1-39.

Сомѕтоск, Ј. Н.

1940. The spider book, revised and edited by W. J. Gertsch. Comstock Publishing Company, New York. 721 pp.

CROSBY, C. R., and S. C. BISHOP

1936. Studies in American spiders: miscellaneous genera of Erigoneae. Festschr. Embrik Strand 2: 52-64.

EDWARDS, R. J.

1958. The spider subfamily Clubioninae of the United States, Canada and Alaska (Araneae: Clubionidae). Bull. Mus. Comp. Zool. 118: 365-436.

ENGELHARDT, V.

Beiträge zur Kenntnis der weiblichen Copulationsorgane einiger Spinnen. Z. Wiss. Zool. 96: 32-117.

EXLINE, H.

1936. Nearctic spiders of the genus Cicurina Menge. Amer. Mus. Novit. No. 850: 1-26.

GERING, R. L.

1953. Structure and function of the genitalia in some American agelenid spiders. Smithson. Misc. Collec. 121(4): 1-84.

GERTSCH, W. J.

1941. New American spiders of the family Clubionidae. II. Amer. Mus. Novit. No. 1148: 1-18.

1949. American spiders. D. Van Nostrand Publishing Company, Inc., New York. 285 pp.

1951. New American linyphiid spiders. Amer. Mus. Novit. No. 1514: 1-11.

GERTSCH, W. J., and I. DAVIS

1946. Report on a collection of spiders from Mexico. V. Amer. Mus. Novit. No. 1313: 1-11.

KASTON, B. J.

1948. Spiders of Connecticut. Connecticut State Geol. Natur. Hist. Surv. Bull. 70: 1-874.

- KASTON, B. J.
 - 1952. How to know the spiders. Wm. C. Brown Company, Dubuque, lowa. 220 pp.

LEVI, H. W.

- 1957a. The spider genera Crustulina and Steatoda in North America, Central America, and the West Indies (Araneae, Theridiidae). Bull. Mus. Comp. Zool. 117: 367-424.
- 1957b. The spider genera *Enoplognatha, Theridion*, and *Paidisċa* in America north of Mexico (Araneae, Theridiidae). Bull. Amer. Mus. Natur. Hist. 112: 1-123.
- 1961. Evolutionary trends in the development of palpal sclerites in the spider family Theridiidae. J. Morphol. 108: 1-9.
- 1965. Techniques for the study of spider genitalia, Psyche **72**(2): 152-158.

MERRETT, P.

1963. The palpus of male spiders of the family Linyphiidae. Proc. Zool. Soc. London 140(3): 347-467.

MUMA, M.

- 1946. North American Agelenidae of the genus Coras Simon. Amer. Mus. Novit. No. 1329: 1-20.
- 1947. North American Agelenidae of the genus *Wadotes* Chamberlin. Amer. Mus. Novit. No. 1334: 1-12.

MUMA, M., and W. J. GERTSCH.

1964. The spider family Uloboridae in North America north of Mexico. Amer. Mus. Novit. No. 2196: 1-43.

PETRUNKEVITCH, A.

1925. External reproductive organs of the common grass spider, *Agelena naevia* Walckenaer. J. Morphol. **40**: 559-573.

SAVORY, T. H.

1928. The biology of spiders. Sidgwick and Jackson, London. 376 pp. WALLACE, H. K.

1942. A study of the *lenta* group of the genus *Lycosa* with descriptions of new species (Araneae, Lycosidae). Amer. Mus. Novit. No. 1185: 1-21.

ABBREVIATIONS USED IN FIGURES

bh basal hematodocha

c conductor

cy cymbium

dh distal hematodocha

e embolus

lsa lateral subterminal apophysis

ma median apophysis

mh middle hematodocha

pc paracymbium

r radix

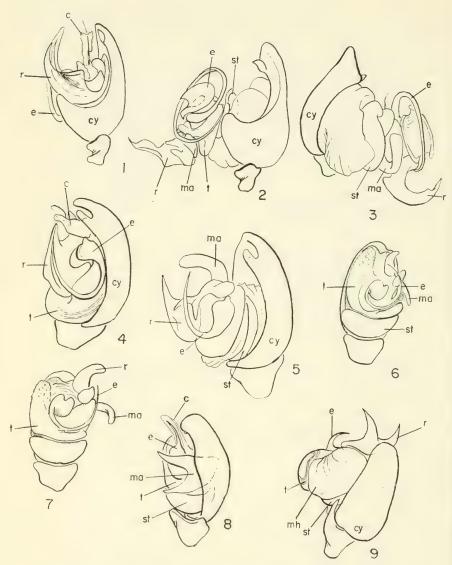
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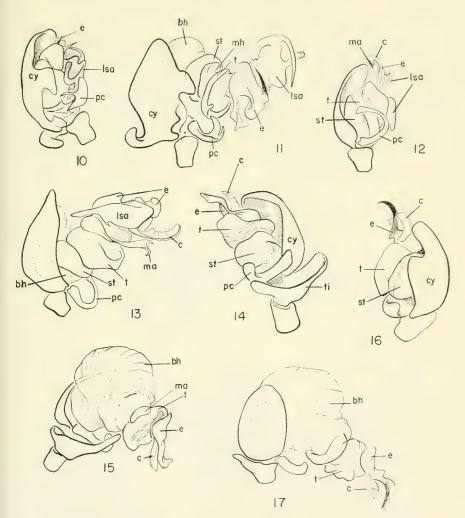
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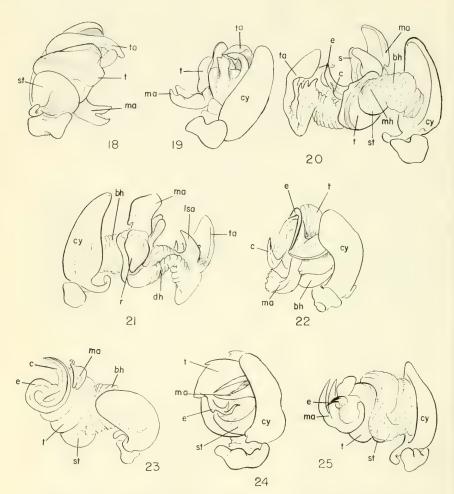
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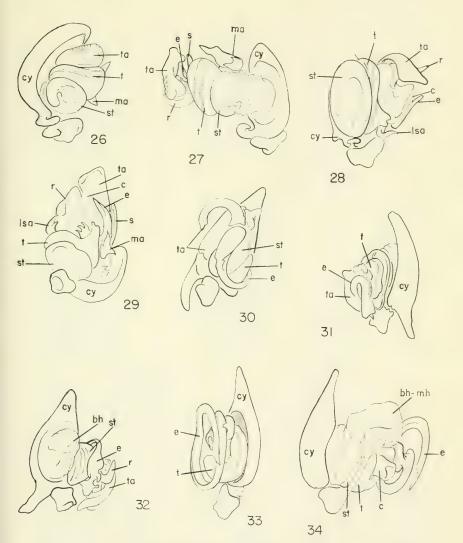
FIGS. 1-3. Steatoda borealis. 1, Mesal view of an unexpanded right palpus. 2, Mesal view of an expanded right palpus. 3, Ectal view of an expanded right palpus. FIGS. 4, 5. Enoplognatha tecta. 4, Ectal view of an unexpanded left palpus. 5, Ectal view of an expanded left palpus. FIGS. 6, 7. Theridion differens. 6, Ventral view of an unexpanded right palpus. 7, Ventral view of an expanded right palpus. FIGS. 8, 9. Theridion frondeum. 8, Ventral view of an unexpanded right palpus. 9, Ventral view of an expanded right palpus.



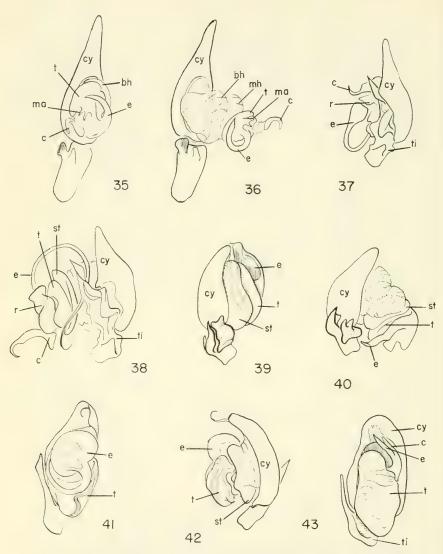
Figs. 10, 11. Drapetisca alteranda. 10, Mesal view of an unexpanded right palpus. 11, Mesal view of an expanded right palpus. Figs. 12, 13. Linyphia marginata. 12, Ectal view of an unexpanded right palpus. 13, Ectal view of an expanded right palpus. Figs. 14, 15. Soulgas corticarius. 14, Ectal view of an unexpanded right palpus. 15, Mesal view of an expanded right palpus. Figs. 16, 17. Ceratinopsidis formosa. 16, Ectal view of an unexpanded right palpus. 17, Dorsoectal view of an expanded right palpus.



Figs. 18-21. Araneus sericatus. 18, Ventral view of an unexpanded right palpus. 19, Mesal view of an unexpanded right palpus. 20, Ectal view of an expanded right palpus. 21, Mesal view of an expanded right palpus. Figs. 22, 23. Argiope trifasciata. 22, Mesal view of an unexpanded right palpus. 23, Dorsomesal view of an expanded right palpus. Figs. 24, 25. Araniella displicata. 24, Ectal view of an unexpanded right palpus. 25, Ectal view of an expanded right palpus.



FIGS. 26, 27. Singa pratensis. 26, Mesal view of an unexpanded right palpus. 27, Ectal view of an expanded right palpus. FIGS. 28, 29. Mangora gibberosa. 28, Ectal view of an unexpanded right palpus. 29, Ventroectal view of an expanded right palpus. FIGS. 30-32. Wadotes calcaratus. 30. Ventral view of an unexpanded right palpus. 31, Ectal view of an expanded right palpus. 32, Mesal view of an expanded right palpus. FIGS. 33, 34. Agelenopsis utahana. 33, Ectal view of an unexpanded right palpus. 34, Mesal view of an expanded right palpus.



FIGS. 35, 36. Tegenaria domestica. 35, Ventral view of an unexpanded right palpus. 36, Ectoventral view of an expanded right palpus. FIGS. 37. 38. Cicurina robusta. 37, Ectal view of an unexpanded right palpus. 38, Ectal view of an expanded right palpus. FIGS. 39, 40. Clubiona bryantae. 39, Ectal view of an unexpanded right palpus. 40, Ectal view of an expanded right palpus. FIGS. 41, 42. Aysha gracilis. 41, Ventral view of an expanded right palpus. 42, Mesal view of an unexpanded right palpus. FIGS. 43. Metacyrba undata, ventral view of an unexpanded right palpus.

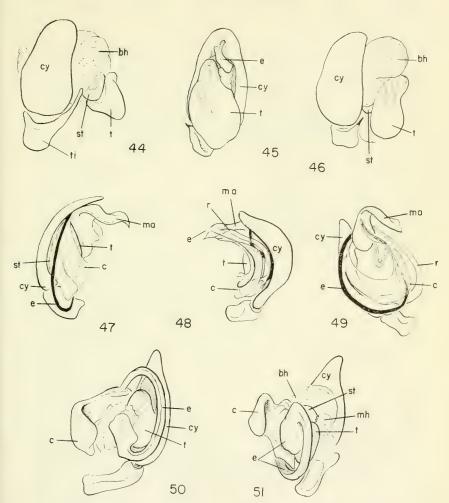


Fig. 44. Metacyrba undata, ectodorsal view of an expanded right palpus. Figs. 45, 46. Tutelina elegans. 45, Ventral view of an unexpanded right palpus. 46, Ectodorsal view of an expanded right palpus. Figs. 47-49. Hyptiotes cavatus. 47, Ectal view of an unexpanded right palpus. 48, Mesal view of an unexpanded right palpus. 49, Ectoventral view of an expanded right palpus. Figs. 50, 51. Dictyna sublata. 50, Mesal view of an unexpanded right palpus. 51, Ventral view of an expanded right palpus.